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THE PRESENCE OF THE BARRED PLUMAGE PATTERN IN THE WHITE LEGHORN BREED OF FOWLS[1]

DR. PHILIP B. HADLEY

In connection with certain inheritance studies, which were undertaken primarily with another purpose in view, a quantity of data are at hand which relate to the constitution of the White Leghorn breed of fowls. In the course of the studies mentioned many crosses were made between the White Leghorn (♂) and females belonging to a variety of black breeds, such as Black Hamburg, Black Minorca, Black Java and Black Spanish. In F_2, and later generations, there appeared a proportion of birds which possessed over the entire body a typical barred plumage pattern. This circumstance led to an inquiry regarding the source of this character in the cases mentioned, and the results of this study appear to warrant the conclusions presented in this paper.

EXPERIMENTAL RESULTS IN F_1

The stock used in these experiments was the best that could be obtained from reliable breeders who had bred the respective varieties for a long period of years. In all the crosses to be mentioned the White Leghorn ♂ was used with black ♀♀. First will be described the results obtained from the mating: White Leghorn ♂ × Black Hamburg ♀.

In the first generation from this cross nothing but white birds was obtained (110 individuals). No birds were, however, pure white. All showed black fleckings which were apparent in some cases only upon close observation. In a small proportion of birds, both males and females, there were present from one to three

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[1] Contribution No. 18 from the Biological Laboratory of the Rhode Island Agricultural Experiment Station, Kingston, R. I.

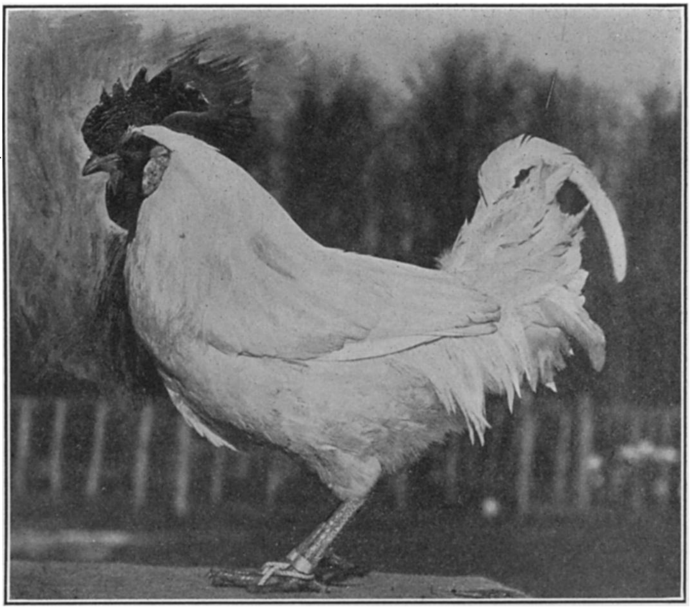

FIG. 1. White Leghorn ♂.

wholly barred or more often partly barred feathers. These usually occurred either among the wing coverts or the tail coverts, although they were occasionally seen in the primary and secondary wing feathers or on the neck. The barring on these feathers was always most distinct at the distal end of the feather, but was never of so good a quality as seen in the Barred Plymouth Rock breed. The "under color" was usually dark. For these F_1 results two series of matings were made and 110 chicks reared. In each series a different White Leghorn ♂ was used, but the results were the same in both cases.

EXPERIMENTAL RESULTS IN F_2

Of the F_1 fowls raised in 1910 one cockerel and five pullets were bred together in 1911. The cockerel was hatched as a pure white bird with no trace of black down feathering. When adult, a single feather showing a buff-yellow bar appeared among the coverts of each wing. Among the saddle feathers were a few showing some buff.

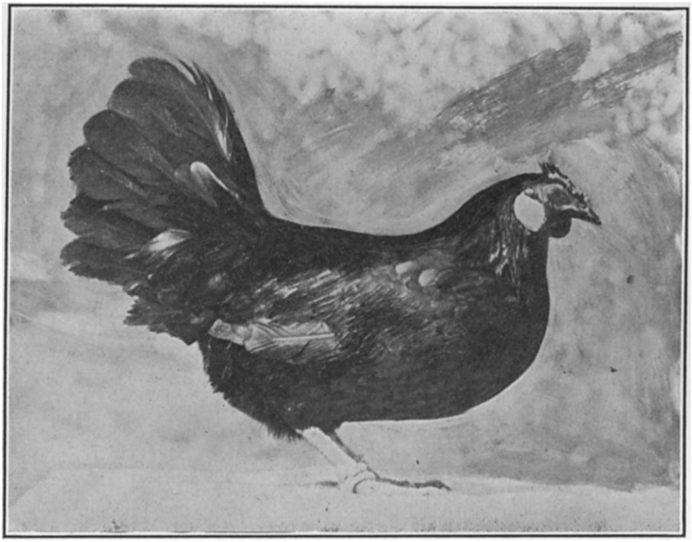

FIG. 2. Black Hamburg ♀.

Of the F_1 females employed in 1911, 201 *G* was a nearly pure white bird but showed a few splashes of black in the saddle feathers and wing coverts. Hen 201 *L* was hatched with a large patch of black down on the back, but eventually became a pure white bird. Hen 202 *G* showed many black splashed feathers on back and wings, while 211 *B* and 211 *V* had a small amount of black ticking. Hen 211 *K* was almost pure white.

The results of these matings showed blacks, grays, whites, splashed whites and barred birds. The blacks possessed as good color as in the original parent stock; the grays appeared as dilute blacks. Some of the whites were pure whites while others showed black ticking. The splashed individuals showed many grades, some being heavily splashed, some slightly. In the barred birds the barring covered the entire body. It was often indistinct, owing to the dark under color, which was never so light as in pure-bred Barred Plymouth Rocks. The barring appeared to correspond fairly well, however, with the barring depicted in early illustrations of years

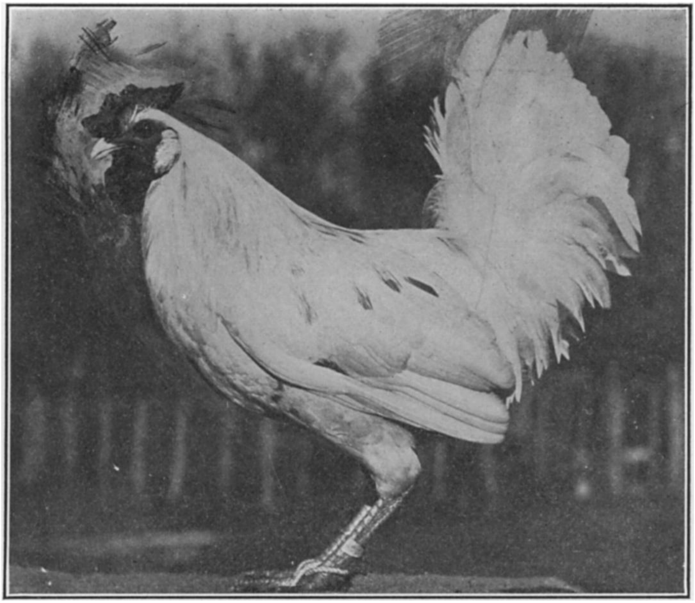

FIG. 3. F_1 Cross-bred ♂.

ago, before the Barred Rocks had been developed to the present state of perfection. The proportions in which these different types appeared in the 1911 series is shown in the accompanying table (Table I).

TABLE I

RESULTS IN 1911 FROM MATING

♂(W. L. ♂ × B. H. ♀) × ♀(W. L. ♂ × B. H. ♀).

Mating	Mother	Total Number.	White	Black			Barred			Gray
				♂	♀	?	♂	♀	?	
314	201 *G*	30	21	0	6	0	2	0	1	0
315	201 *L*	22	16	0	1	0	2	0	3	0
316	202 *G*	6	5	0	1	0	0	0	0	0
317	211 *B*	17	15	0	1	0	0	0	1	0
340	211 *K*	23	18	0	0	2	0	0	0	3
341	211 *V*	19	15	0	0	1	0	2	0	1
Totals		117	90	0	9	3	4	2	5	4
Expected......		117	$87\frac{3}{4}$	0	$7\frac{5}{16}$		$14\frac{10}{16}$	$7\frac{5}{16}$		
Totals		117	90		16			11		
Expected......		117	$87\frac{12}{16}$		$7\frac{5}{16}$			$21\frac{15}{16}$		

[2] Includes the four gray fowls.

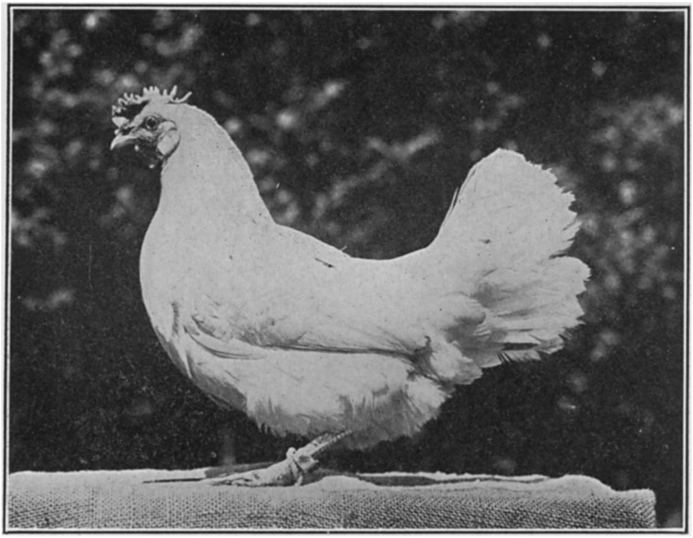

FIG. 4. F_1 Cross-bred ♀.

Before discussing this case, the results of a similar mating of other F_1 birds, in 1912, may be presented. The F_1 male was 8 *L*, mated with his sisters, 8 *B*, 8 *G*, 8 *H* and 8 *I*, all of which resembled the F_1 females in the 1911 series.

TABLE II

RESULTS IN 1912 FROM MATING

♂(W. L. ♂ × B. H. ♀) × ♀(W. L. ♂ × B. H. ♀).

Mating No.	Total No.	White	Black			Barred		
			♂	♀	?	♂	♀	?
456	18	13	0	1		2	1	1
457	13	8	0	1		3	0	1
458	14	10	0	1		2	1	0
459	25	21	0	0		2	1	1
460	67	54	0	3	1	5	3	1
Totals................	137	106	0	6	1	14	6	4
Expected...........		$102\frac{12}{16}$	0	$8\frac{9}{16}$		$17\frac{2}{16}$	$8\frac{9}{16}$	
Totals................	137	106	7			24		
Expected...........		$102\frac{12}{16}$	$8\frac{9}{16}$			$25\frac{11}{16}$		

DISCUSSION

It may now be asked how the presence of the barred

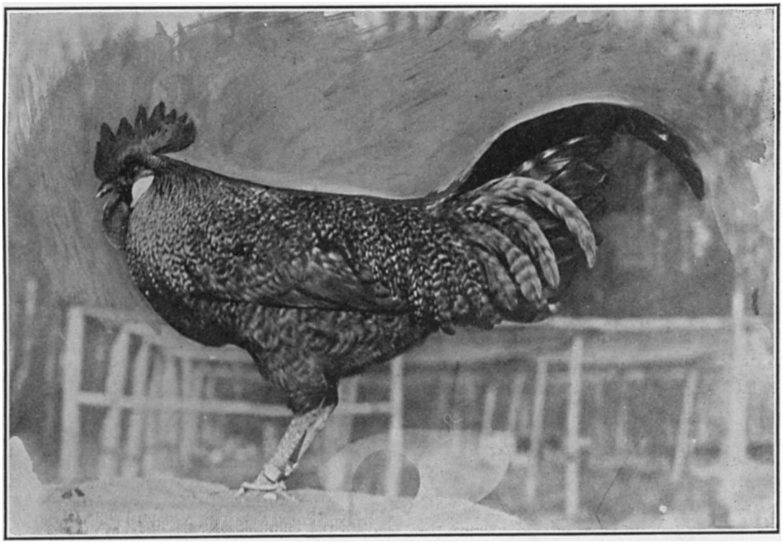

FIG. 5. F_2 Barred ♂.

birds is to be explained. Since it would be impossible for the Black Hamburg females to carry the barring factor, unless they also possessed an inhibition for barring, the obvious conclusion is that this pattern came from the White Leghorn. We may tentatively assume then that the W. L. ♂ is homozygous for barring, and attempt to ascertain to what extent the experimental results agree with the expected results in such a case.

First, it may be said that the W. L. breed in all probability carries a factor for black pigmentation (N), and also a factor which inhibits the manifestation of black in the plumage (I). Furthermore we may assume that it possesses a color factor C, and that the male is homozygous for the absence of the female sex factor, F, for which the females are heterozygous. In addition to this we may assume that in gametogenesis the barring factor, B, is repelled by F. There is no reason for assuming that the W. L. ♂ is other than homozygous for I. We may then write the zygotic formulas of the W. L. ♂ as:

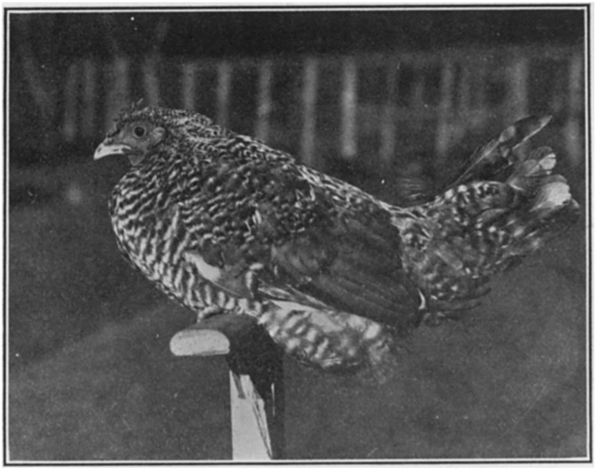

FIG. 6. F_2 Barred ♀.

$$C_2B_2N_2f_2I_2$$

forming gametes

$$CBNfI \cdot CBNfI.$$

As to the zygotic constitution of the Black Hamburg ♀♀ there is no reason for supposing that they contain either B or I, although they do contain C and N; also they may be looked upon as heterozygous for F. We may therefore write their zygotic formula as

$$C_2b_2N_2Ffi_2$$

forming gametes

$$CbNFi \cdot CbNfi.$$

But, since, in all probability, none of the birds in these experiments lacks the factors C or N, we may leave these out of consideration, thus writing the W. L. ♂ formula:

$$B_2f_2I_2$$

forming gametes

$$BfI \cdot BfI,$$

and the B. H. ♀ formula as

$$b_2Ffi_2$$

forming gametes

$$bFi \cdot bFi.$$

The mating then becomes

W. L. BfI BfI
B. H. bFi bFi

B_bf_2Ii = white ♂♂, heterozygous, for barring and inhibiting factor.
$BbFfIi$ = white ♀♀, heterozygous, for barring and inhibiting factor.

In other words, the F$_1$ from mating of W. L. ♂ × B. H. ♀ gives birds that are all white, but heterozygous for *B* and *I*. The fact that some F$_1$ birds put up barred feathers may be explained on the ground that the dominance of the inhibiting factor (*I*), in heterozygous condition, was not complete. Where a little black was permitted to show, there it filled the pattern of an already barred feather.

What now takes place when the F$_1$ whites are mated among themselves? The F$_1$ males with the zygotic constitution $BbffIi$ form gametes BfI Bfi bfI bfi. The F$_1$ females with the zygotic constitution Bb Ff Ii form gametes BfI bFi Bfi bFI. The mating of the F$_1$ stock may therefore be represented:

♂ $BfI \cdot bfi \cdot Bfi \cdot bfI$
♀ $BfI \cdot bFi \cdot Bfi \cdot bFI$ giving in F$_2$

♂♂	$B_2f_2I_2$	(1)	White, homozygous for *B* and *I*.
	Bbf_2Ii	(2)	White, heterozygous for *B* and *I*.
	B_2f_2Ii	(2)	White, homozygous for *B;* heterozygous for *I*.
	Bbf_2I_2	(1)	White, heterozygous for *B;* homozygous for *I*.
	Bbf_2i_2	(1)	Barred, heterozygous for *B;* no *I*.
	$B_2f_2i_2$	(1)	Barred, homozygous for *B;* no *I*.
♀♀	$Bb\ Ff\ Ii$	(2)	White, heterozygous for *B* and *I*.
	$bb\ Ff\ i_2$	(1)	Black, no *B* nor *I*.
	$Bb\ Ff\ I_2$	(1)	White, heterozygous for *B;* homozygous for *I*.
	$bb\ Ff\ Ii$	(2)	White; no *B;* heterozygous for *I*.
	$Bb\ Ff\ i_2$	(1)	Barred, heterozygous; no *I*.
	$bb\ Ff\ I_2$	(1)	White, no *B;* homozygous for *I*.

The data presented above may be summarized as follows:

Characters	♂	♀	Total
White	6	6	12
Black	0	1	1
Barred	2	1	3
Totals	8	8	16

In other words, among every 16 birds in F_2 we might expect to find 12 whites, 3 barred and 1 black. The whites should be equally divided between the sexes; of the three barred birds, two should be male and one female; the one black should be a female. Moreover, one of the barred males should be homozygous for this factor, while the other male and the female should be heterozygous. Other birds, including both males and females, should carry the barring factor but not manifest the pattern since they will also be either homozygous or heterozygous for the inhibiting factor, *I*.

Having thus outlined what we should expect to see result in F_2, provided the original W. L. cockerel was actually homozygous for barring and also possessed factors *C, N* and *I,* we may now attempt to ascertain to what extent these theoretical results agree with the experimental data and furnish an interpretation for them.

First, referring back to Table I, it is apparent that the expected 3:1 ratio of a white × black cross is fairly closely realized among the 117 birds included in this table. Actual results were 90 white: 27 dark, while the expected are 88 white: 29 dark. Whereas we should expect only 7 + blacks, all females, we actually have 12 blacks (16 including the grays), including 9 females and 3 of undetermined sex. In part explanation of the discrepancy it may be said, however, that in very young chicks it is impossible to distinguish the blacks from the barred. In case chicks die during the first week of life, all those which would later develop barring must be described as black. It therefore can not be doubted that several of the birds described as black were actually barred. The only way to avoid this difficulty is to embody in the tables no chicks which die under three weeks of age. This plan was adhered to in the collection of data presented in Table II.

Regarding the barred birds, it is clear that more are called for than actually appeared; but, as already explained, the number would probably have been made up by addition of birds from the blacks, if these chicks had lived long enough to develop their barring. It is apparent, however, that the ratio of males to females is in the right sense.

Turning now to the results of similar matings presented in Table II, it is apparent that the experimental results conform more closely to the expected. In this case all the chicks were over three weeks old when described. The obtained ratio of whites to blacks is 106:31, while the expected is 102:35. The actual ratio of black to barred birds was 7:24, while the expected was 8 + : 25 +. As was to be expected, no black males appeared, while the number of barred males was approximately twice the number of the barred females (14:6), the expected being 17 + : 8 +.

It is thus clear that when only chicks over three weeks old are included in the tables, the actual and the expected ratios find close agreement, and appear to demonstrate the correctness of the view that the male White Leghorn fowl is homozygous for the barred plumage pattern. Evidence similar to that presented above has been secured from matings of White Leghorn ♂ with Black Minorca, Black Java and Black Spanish hens. Crosses involving the White Leghorn ♀ have not yet been made, but it seems likely that these fowls are heterozygous for the barred character, which probably follows lines of inheritance similar to the barring of the Barred Plymouth Rock breed. In the White Leghorn breed, of which several different males have now been tested, the barred pattern appears to exist as a cryptomere, much as in the breed of

White Plymouth Rocks, the chief difference in these two races being that whereas the white of the White Rock is a "recessive white," occasioned, in all probability, by the dropping out of a color factor, the White Leghorn is a so-called "dominant white," determined by the presence of an inhibitor acting upon one or both of the color factors, which also appear to be present in this breed.

CONCLUSIONS

These results serve to confirm suggestions made by Davenport[3] regarding the presence of barring in some of his White Leghorn stock, and also to explain some of the results obtained by Hurst[4] in matings, which involved the White Leghorn breed. They also help to explain some of those cases known to many poultrymen[5] in which barring (the "cuckoo marking") has resulted from the crossing of black (or dark) with white breeds in which the presence of the barred plumage pattern was not suspected.

Obviously this work has no bearing upon the *origin* of the barred pattern. It merely indicates that the White Leghorn breed of fowls, as studied, carries factors for both black and barring. The failure of the black to show depends upon the action of the inhibitor, *I*, while the barred pattern can appear only in the presence of the uninhabited *N* or *C*.

March 4, 1913

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[3] Davenport, C. B., "Inheritance in Poultry," Publication No. 52 of the Carnegie Institution of Washington; Papers of the Station for Experimental Evolution, No. 7, 1906.

"Inheritance of Characters in the Domestic Fowl," Publication No. 121 of the Carnegie Institution of Washington; Papers of the Station for Experimental Evolution, No. 14, 1909.

[4] Hurst, C. C., Report II to the Evolution Committee of the Royal Society, London, England, 1905.

[5] Wright, L., "New Book of Poultry," London (Cassell), 1905.